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North American Rhabdocoela and Alloeocoela. 6

A Further Study of *Mesostoma*

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The rhabdocoel genus *Mesostoma* is widely distributed in the fresh waters of the world, especially those of temporary nature. The genus was reviewed by Ferguson and Hayes (1941) who recognized 22 valid species (but omitted some regarded by other persons as valid) and listed nearly 100 additional names placed in the genus in the past, since transferred to other genera or unidentifiable on available information. Since their article there have been described: *M. benazzii* Papi, 1949, Italy; *M. ewerum* Eveline Marcus, 1951, Natal; *M. inversum* Beauchamp, 1954, Ruanda, Africa; *M. vernale* Hyman, 1955, North Carolina; and *M. curvipenis* Hyman, 1955, Delaware. As previously noted (Hyman, 1955), *M. macroprostatum* Hyman (1939b) should be removed from the genus, and in the present article it is suggested that *M. macropenis* Hyman (1939a) is only a form of *M. ehrenbergi*. With the two present species there remain seven endemic species of *Mesostoma* and the cosmopolitan species *M. ehrenbergi* (Focke, 1836) known from North America.

The genus belongs to the family Typhloplanidae of the group termed Lecithophora by Graff (1905), Bulbosa by Meixner (1924), and Neorhabdocoela by Meixner (1938). I am inclined, with Ernesto Marcus (1954), to retain the name Rhabdocoela for this group, emended to exclude the Catenulida and Macrostomida.

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For All Figures

1, Rod tract; 2, pharynx; 3, mouth; 4, gonopore; 5, capsule; 6, testis; 7, intestine; 8, brain; 9, epidermis; 10, pigment; 11, yolk glands; 12, nerve tract; 13, ovary; 14, proximal oviduct; 15, seminal receptacle; 16, distal oviduct; 17, glands; 18, penis bulb; 19, seminal part of penis bulb; 20, prostatic part of penis bulb; 21, ejaculatory duct; 22, penis papilla; 23, common antrum; 24, copulatory bursa; 25, bursal canal; 26, eyes; 27, depression; 28, prostatic glands; 29, sperm duct; 30, rhammite-forming cells; 31, anterior copulatory bursa; 32, posterior copulatory bursa; 33, common vitelline duct; 34, uterus; 35, reticulate cells; 36, seminal vesicle; 37, prostatic vesicle; 38, diverticulum; 39, spermiducal vesicle.

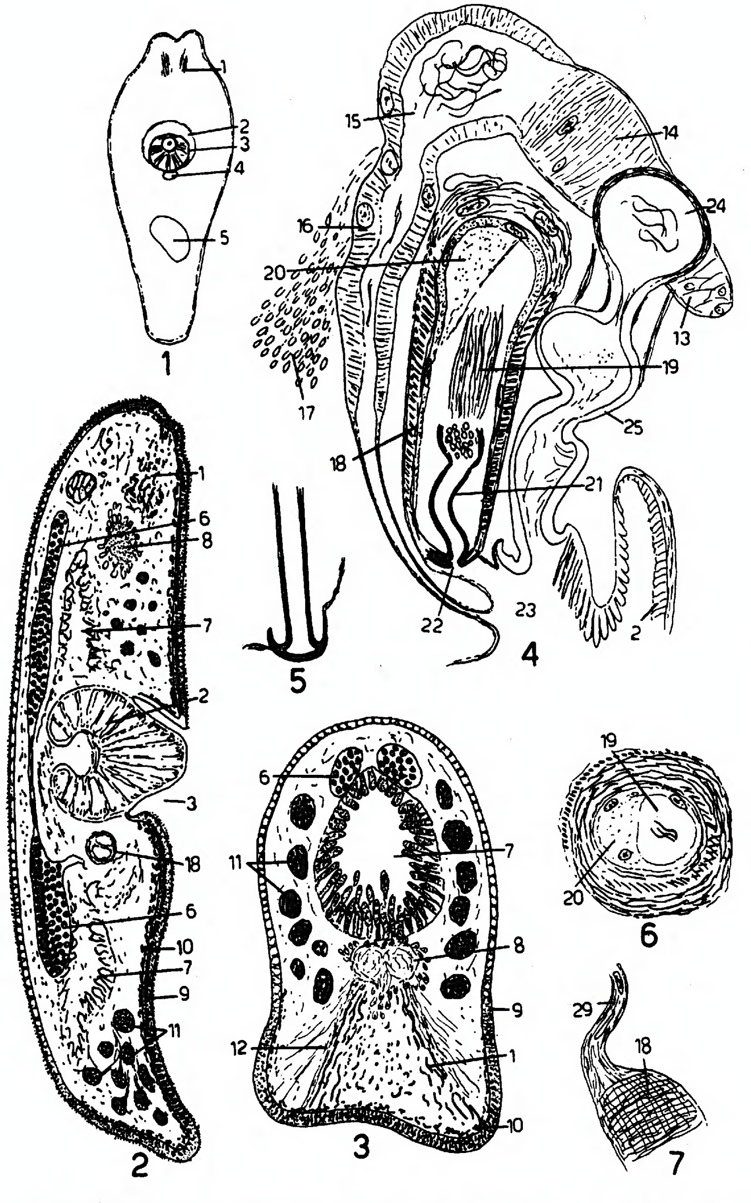
Mesostoma andrewsi, new species

Figures 1–7

Several specimens of this species were sent by Robert Rausch, Arctic Health Research Center, Anchorage, Alaska. They had been collected in August and September, 1954, in the interior of St. Andrew's Island in the Bering Sea, in fresh-water pools, on wet tundra, and in vegetation along streams.

The worms (preserved) are about 2 mm. long and of a very dark brown color. The shape of a preserved specimen, shown in figure 1, probably bears no relation to the shape in life. As no notes are available on living worms, it cannot be stated whether the two lobes at the anterior end are present in life, but evidently they are related to the rod tracts, which appear in cleared specimens as two dark streaks in the anterior end. Sensory depressions are wanting, but a pair of eyes was found in the sections, although not detectable in the whole worms.

Six worms were sectioned but were found in poor histological condition. The entire surface appears ciliated (fig. 2). The dorsal epidermis is much thinner than the ventral epidermis (figs. 2 and 3), is devoid of rhabdites, and consists of hourglass-shaped cytoplasmic strands interspersed with vacuoles. Towards the sides the epidermis increases in height, begins to show rhabdites as black bodies, and becomes more cytoplasmic and less vacuolated. The ventral epidermis is quite tall and thickly provided with rhabdites (figs. 2 and 3). The ventral epidermis is also underlain by much pigment that extends part way up the sides of the animals but is practically lacking dorsally. A greater pigmentation ventrally than dorsally is known in other mesostomines and may indicate a habit of swimming at the surface film, ventral side up. A subepidermal musculature appeared to be present, but details cannot be furnished because of bad fixation. For the same reason little can be said of the interior histology except for the presence of two rod tracts extending from the



FIGS. 1–7. *Mesostoma andrewsi.* 1. Dorsal view of preserved specimen. 2. Longitudinal parasagittal section. 3. Oblique section through the brain, showing rhammite tracts. 4. Sagittal view of copulatory apparatus, represented as if on one plane. 5. Penis papilla everted. 6. Transverse section through the upper part of the penis bulb. 7. Proximal end of penis bulb, showing entrance of sperm duct.

brain to the anterior margin (figs. 2 and 3) and accompanied on their outer side by a large nervous tract. The two rod tracts are not sharply separated from each other. They consist of long, sinuous filaments that presumably represent rhammites.

Despite the poor fixation the general structure of the reproductive system was ascertained. Each of the two testes consists of an anterior and posterior lobe connected by a non-spermatic strand (fig. 2). The testes occur just beneath the dorsal wall above the digestive tract, with the anterior lobes reaching the level of the brain (fig. 3) and the posterior lobes situated above the copulatory apparatus. A sperm duct leaves the ventral side of the anterior part of each posterior lobe (fig. 2), but the ducts could not be traced into the penis. The yolk glands form the usual numerous follicles in the sides of the animal (figs. 2 and 3), but their ducts also were not traceable to the copulatory apparatus.

The copulatory apparatus forms the usual complex directly behind the pharynx, here opening in common with the mouth as in many other species of *Mesostoma* (fig. 4). It was reasonably well made out in one series of sagittal sections on which figure 4 is based and which has been made the type of the species. The apparatus consists, as typical of the genus, of three parts, the copulatory bursa, the penis, and the female tract, occurring in that order from the pharynx posteriorly but not on the same plane, although so represented in figure 4. The penis bulb is to the left of the other structures. All three structures open ventrally into a large common antrum that opens midventrally by the common gonopore, easily seen in whole mounts (fig. 1) as an oval pit at the posterior edge of the mouth.

The copulatory bursa or sac consists of a canal leading dorsally from the common antrum and terminating blindly in a spherical sac with a thick muscular wall and serving as a temporary receptacle for sperm received at copulation. The copulatory sac connects with the bursal canal by a narrowed muscular tube. The canal itself presents two expansions, but these were not evident on the other sets of sections, hence I cannot state that they are characteristic of the species. The wall of the bursal canal stained homogeneously, and therefore its histological construction could not be ascertained.

The penis consists mainly of an oval muscular bulb lined by a syncytial (plasmatic) layer and having a wall of inner and outer longitudinal fibers with a diagonal layer between. The proximal part of the bulb is heavily supplied with circular fibers much in evidence in all sections (fig. 6). Proximally the bulb is about evenly divided into a spermatic half and a prostatic half (fig. 6), but the latter could not be followed distally. The spermatic part contains a heavy bundle of sperm. The bulb terminates distally in a small cuticularized penis papilla which is shown in folds in figure 4, but can be projected, as in figure 5, from another series of sections. A cuticularized tube leads inward from the penis papilla, receiving into its open inner end some eosinophilous granules, no doubt the prostatic secretion. In this series of sections the sperm duct could not be followed into the penis bulb, but in another set could be seen entering the summit of the bulb (fig. 7). In no case could prostatic glands be detected or followed into the penis bulb. A cuticularized ejaculatory duct in the interior of the distal part of the penis and leading into the penis papilla is known in some other species of *Mesostoma* but is not a generic character.

The female tract follows the usual course and presents nothing distinctive. It begins blindly with the ovary which projects anteriorly to the left of the copulatory sac and is continuous with the proximal oviduct, composed as usual of a succession of disciform cells. This is succeeded by the seminal receptacle, an expansion containing sperm and serving as the permanent storehouse of sperm received at copulation. There follows the distal oviduct, usually called ductus communis, more properly ovovitelline duct. This has walls of striated cytoplasm with occasional large round nuclei and typically receives into its anterior wall the common vitelline duct from the yolk glands; but this could not be traced in any of the available sections. A number of glands were seen related to the posterior wall of the ovovitelline duct as shown in figure 4. Distally this duct narrows to a very thin-walled tube that enters the posterior end of the common antrum. The usual two uteri, not shown in any of the figures, were seen extending posteriorly from the common antrum and containing the dark brown capsules, collapsed into the hemispherical shape usual in preserved *Mesostoma.*

Steinböck (1932) listed six species of *Mesostoma* from arctic regions: *productum, lingua, craci, maculatum, platygastricum,* and *murmanicum,* of which the last three have not been found elsewhere. To this list must be added *M. arcticum* Hyman, 1938, taken at Churchill, Manitoba, Canada, and later found in alpine bogs in the Medicine Bow Mountains, Wyoming. The present species resembles *M. productum* in having eyes, paired rhammite tracts, and stronger pigmentation ventrally than dorsally, but is quite different as regards form of the testes, penis bulb, and copulatory bursa (last description of *M. productum* by Gelei, 1933). In *M. lingua,* also with eyes and paired rhammite tracts, the lack of a cuticularized ejaculatory duct is sufficient distinction from *M. andrewsi. Mesostoma craci* is a large (15 mm.), somewhat transparent species with a long, tubular penis papilla. *Mesostoma maculatum* lacks eyes and is distinctively marked with white spots. *Mesostoma platygastricum* shows most resemblance to *andrewsi* of any of the arctic species, being more strongly pigmented ventrally than dorsally, having testes of a similar shape, and also a similar penis with sinuous cuticularized ejaculatory duct; but the eyes of *platygastricum* are much better developed than in *andrewsi*, the gonopore is separate from the mouth, and the form of the copulatory sac differs altogether. The original and only description of *M. platygastricum* is so sketchy that comparisons are difficult. *Mesostoma murmanicum* probably does not belong to the genus *Mesostoma*. *Mesostoma arcticum* presents many peculiarities of structure. It is improbable that *M. andrewsi* could be identical with other arctic species of the genus.

Mesostoma andrewsi is distinguished from other species of the genus by the combination of greater pigmentation ventrally than dorsally, paired rod tracts, poorly developed eyes, lack of sensory depressions, testes formed into an anterior and a posterior lobe, spherical copulatory bursa exiting by way of a muscularized constriction into a long and broad bursal canal, oblong penis with sinuous cuticularized ejaculatory duct terminating in a very small cuticularized penis papilla, slight development of the prostatic part of the penis bulb, and gonopore opening in common with the mouth.

HOLOTYPE: One set of the sagittal sections deposited in the invertebrate section of the American Museum of Natural History; also one whole mount deposited.

Mesostoma californicum, new species

Figures 8–15

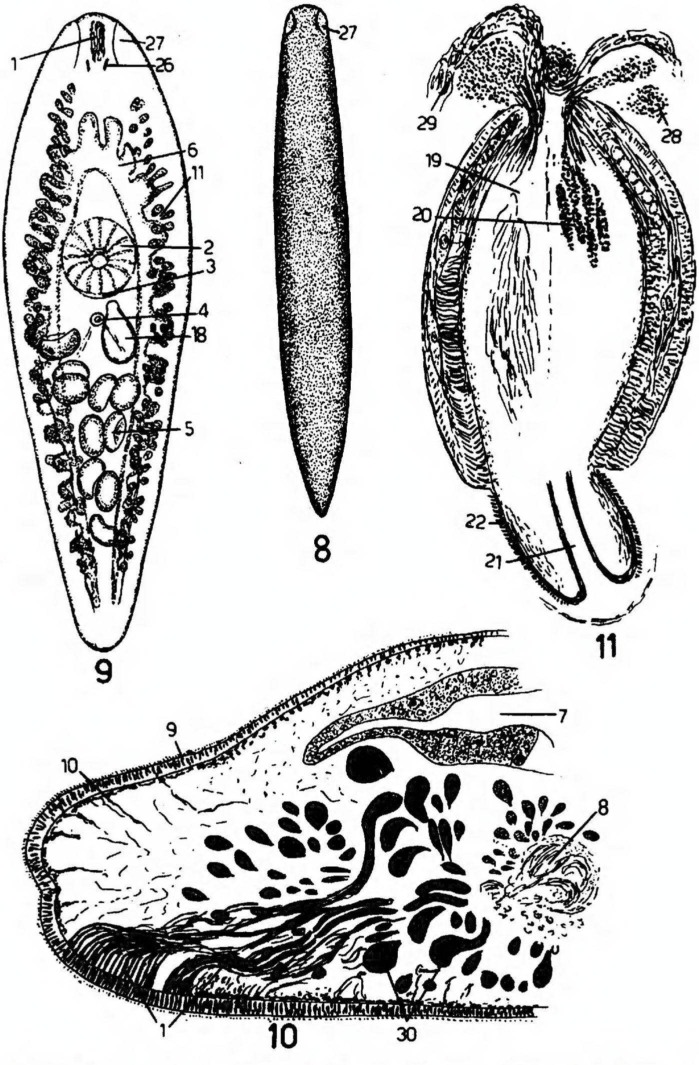
A number of specimens were sent alive by Enid Larson and Richard Tetley, Unified School District, Carmel, California, who had collected them in temporary rain pools in the vicinity of Carmel during the last week of February, 1956.

The living worms when moving extended were about 5 mm. long, of elongated slender shape with rounded anterior end, having a semicircular depression on each side, and pointed posterior end (fig. 8). The worms were active and restless and glided about rapidly. The color was uniform dark gray, lighter in the two anterior depressions. Eyes were not evident in the living worms but were dimly seen in stained whole mounts (fig. 9) and in sections (fig. 15) were found well developed. The body is of perfectly smooth contour in life but on fixation was thrown dorsally into longitudinal ridges (fig. 13) in most specimens; hence the occurrence of such ridges based on preserved specimens alone cannot be regarded as of any taxonomic value.

The general features of organization as seen in a stained whole mount are shown in figure 9. In the anterior end between the two depressions is found a strong median rod tract. The eyes are located near the posterior end of this. The rosette pharynx is situated well anterior to the middle of the worm, and behind and well separated from it is seen the common gonopore. The follicular yolk glands form small clusters arranged in a longitudinal tract on each side. The area between these tracts posterior to the gonopore is filled with the hard-shelled egg capsules, which in this species have the shape of biconvex disks (fig. 14). The testes give off large lateral lobulations and are confluent anteriorly, at least in some specimens (fig. 9).

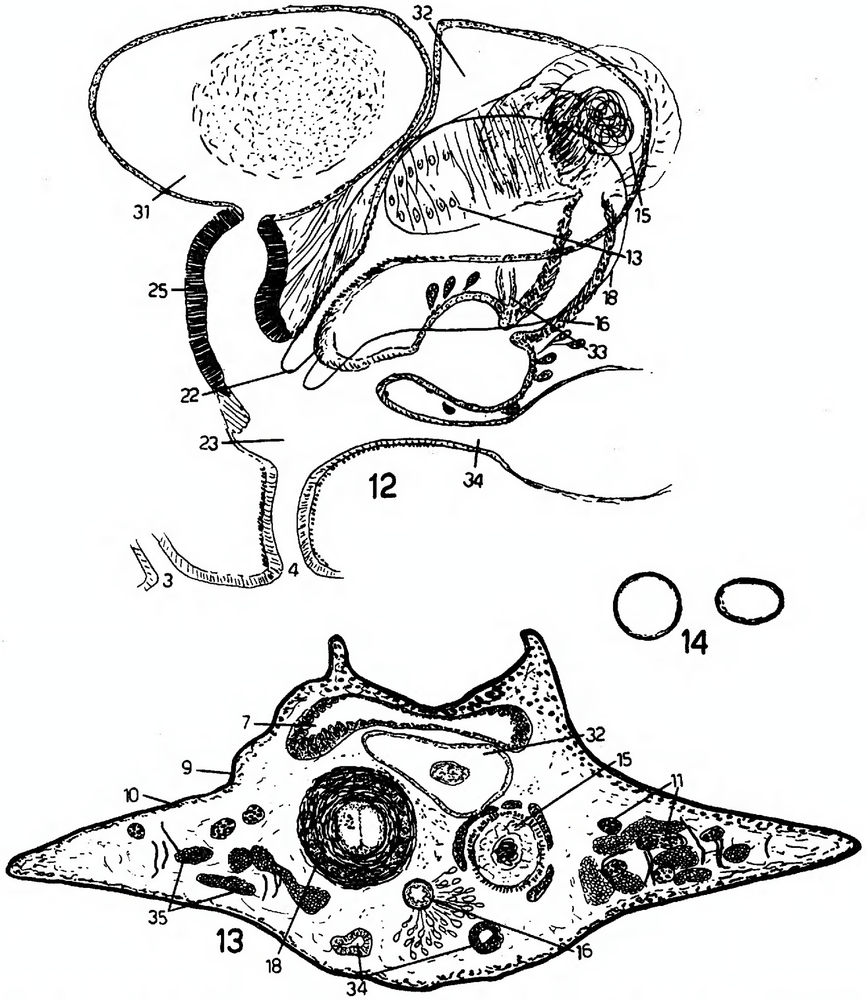
The epidermis is ciliated throughout and is slightly taller ventrally than dorsally, especially on the anterior end (fig. 10). It is everywhere very dark, apparently containing pigment, and pigment is also present beneath the entire epidermis, about equally on dorsal and ventral sides. A median highly developed rod tract is present, shown in median sagittal section in figure 10. The tract extends between the brain and the ventral side of the anterior tip and consists of large, darkly staining pyriform masses, presumably rhammite-forming cells, and sinuous tracts proceeding anteriorly from these and curving ventrally to open into the here taller epidermis. The depressions at the anterior end did not show any histological differentiation in sections. The eyes, located as usual near the brain, are shown in transverse section in figure 15. Throughout the interior were noticed large cells with reticulate cytoplasm and staining a bright blue with hematoxylin. They are shown in figures 13 and 15. Their nature could not be ascertained.

The copulatory apparatus, located immediately behind the pharynx, opens ventrally by a separate gonopore shortly behind the mouth (fig. 12). The copulatory apparatus, as seen from the left side, is shown in general sagittal view in figure 12, and details of the penis are given in figure 11. The apparatus is remarkable in having two copulatory bursae, both of which are further very large. The anterior bursa arises from the common genital antrum just behind the pharynx by a very muscular stalk surrounded by a strong layer of circular fibers. The stalk constricts as it enters the large rounded bursa with a thin wall of indeterminate construction. The second bursa springs from the dorsal wall of the genital antrum just behind the anterior bursa by a more slender, less muscular stalk, which still has evident circular fibers. This widens in funnel fashion to enter the posterior bursa, of about the same size as the anterior one



FIGS. 8–11. *Mesostoma californicum.* 8. Dorsal view of living worm. 9. Ventral view of stained whole mount. 10. Sagittal section of anterior end, showing rhammite tract. 11. Sagittal section of penis bulb.

but squeezed by the latter into an irregular shape. Both bursae in all sections contain a large mass of slightly eosinophilous material that definitely does not consist of sperm. The female tract springs from the posterodorsal wall of the antrum by a narrow tube that widens into a cordiform chamber surrounded by gland cells; from this a muscularized tube ascends and opens into the seminal receptacle from which there projects



FIGS. 12–14. *Mesostoma californicum.* 12. Sagittal view of copulatory apparatus, seen from the left side, anterior end to left. 13. Transverse section through posterior part of copulatory apparatus. 14. Capsule seen from above and from the side, showing biconvex oval shape.

anteriorly to the right side of the penis the proximal oviduct of disciform cells continuous with the ovary. The common vitelline duct enters the female tract just proximal to the cordiform expansion (fig. 12). Just ventral to the opening of the female tract into the antrum are seen the two uteri extending posteriorly.

The penis (fig. 11) is an oval body lying in a horizontal position to the left of the female tract with its papilla projecting into about the center of the common antrum. The penis consists mainly of the penis bulb, having the usual wall of complex muscle fibers, mostly inner and outer longitudinal fibers with diagonal or spiral layers between, showing plasmatic areas containing nuclei. The interior of the penis bulb is longitudinally divided equally into a seminal half containing sperm and a prostatic half containing prostatic secretion. Sperm ducts and prostatic glands enter together at the summit of the bulb. A strong indentation separates the bulb from the penis papilla, a rounded projection covered externally with circular muscle fibers and containing centrally a cuticularized ejaculatory duct.

Figure 13 shows a cross section through the uteri and the seminal receptacle which is shown surrounded by the usual coarsely granular gland cells. The two dorsal ridges are artifacts resulting from contraction on fixation. Near the dorsal surface is seen the intestine, below that the posterior copulatory bursa, and below that on the left a section through the penis bulb, on the right a section through the seminal receptacle. Below, about centrally, is the distal oviduct, with attendant gland cells, and below that are the two uteri. Testes seemed to be absent from this series of sections. Yolk glands are seen laterally and near them the large reticulate cells already mentioned.

The testes are a pair of elongated cylinders with large lateral lobulations; they are indicated in figure 9. In cross sections they usually appear as four rounded masses just beneath the dorsal body wall; the median masses are the testes, the lateral ones the lobulations. The testes are confluent anteriorly.

The capsules of this species are distinctive in that they have the form of biconvex disks, that is, appear circular in one view, oval when rotated 90 degrees (fig. 14).

Mesostoma californicum differs from all other species of the genus in having two copulatory bursae.

HOLOTYPE: One slide of sagittal sections deposited in the invertebrate section of the American Museum of Natural History; also one whole mount.

Mesostoma ehrenbergi (Focke, 1836)

Figures 16, 17

A large number of preserved specimens were sent by R. B. Brunson of Montana State University, who had collected them in glacial potholes in the vicinity of Missoula, Montana, between May 23 and June 7, 1956. The worms were stated to have been slightly over 10 mm. in length alive.

This is of course a very well-known cosmopolitan species but in view of the fact that Ruebush (1940) and Husted and Ruebush (1940) took the position that North American representatives differ in several definite ways from the nominal European form and constitute a subspecies *wardii,* it was thought desirable to make a detailed study of the specimens, and a number of sections were prepared.

In the first place it is claimed by Husted and Ruebush that North American specimens do not exceed a length of 7 mm., but the present specimens and those of Muliak (1947) from Utah were 10 mm. long and hence compare favorably with European specimens. Luther's specimens (1904) from Finland, on which he based the best available description of the histological details of the species, were 10 to 11 mm. long when fully extended, alive.

Then Husted and Ruebush assert that in North American specimens the seminal receptacle is not the usual expansion of the oviduct but a stalked vesicle set off from the oviduct, and further that stalk and sac of the copulatory bursa are equally muscular. Figure 16 gives a median sagittal view of the female organs of the Montana specimens. The seminal receptacle is seen to be an enormous expansion of the oviduct as in European specimens, and the stalk of the copulatory bursa is far more muscular than the sac, being encircled by strong muscle fibers.

Whether the penis enters the anterolateral wall of the common antrum as in European specimens or the posterolateral wall as claimed by Husted and Ruebush for North American specimens is difficult to answer from preserved specimens because of contractions and distortions caused by fixation. However, in all of several series of sections the penis papilla was found in the antrum below the entrance of the bursa stalk, and as the bursa is the most anterior part of the copulatory complex this indicates the projection of the penis papilla into the antrum from in front. The diverticulum of the ejaculatory duct asserted by Husted and Ruebush to be absent in North America specimens is also present in the Montana material (fig. 17). Spermiducal vesicles ("false seminal vesicles"), that is, expanded sperm-filled terminations of the sperm ducts, are conspicuously present in the Montana material, supposed by the authors mentioned to be wanting in North American specimens. One such spermiducal vesicle is shown in figure 17.

In short, it has been impossible to find any of the alleged differences between Montana and European specimens of *M. ehrenbergi.* Dr. E. Ruffin Jones of the University of Florida, a specialist on rhabdocoels, permits me to say that he has examined specimens of *M. ehrenbergi* from various localities in Virginia and Florida and all of them seemed to fit

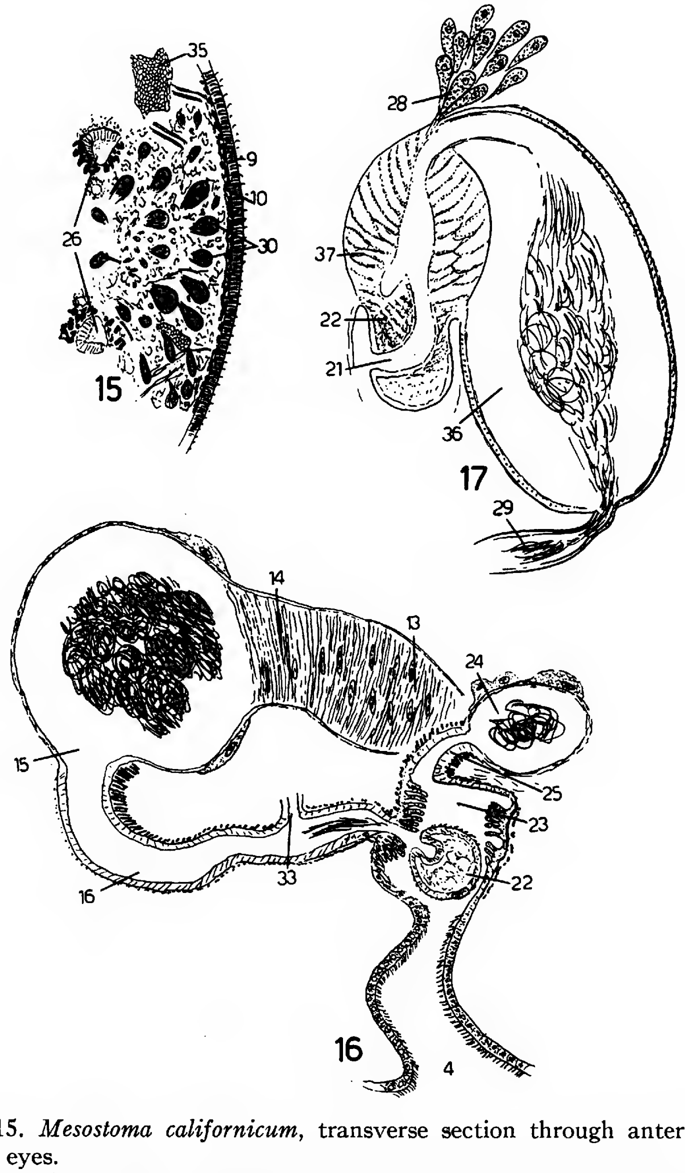


FIG. 15. *Mesostoma californicum*, transverse section through anterior end, showing eyes.

FIGS. 16, 17. *Mesostoma ehrenbergi*. 16. Female part of the copulatory apparatus, in sagittal view. 17. Penis.

the description of the European form. "If morphological differences exist they must be very minor." Neither Dr. Jones nor I made any study of the chromosomes. I may further mention that a whole mount of *M. ehrenbergi* from Green Lake, Seattle, Washington, kindly sent by Dr.

Trevor Kincaid, also appeared to fit the European form. This was removed from the slide and sectioned sagittally but had been so greatly flattened that the copulatory apparatus was unsatisfactory for study. At least it could be ascertained that the seminal receptacle of the specimen is constituted of the usual expansion of the oviduct, and further that the ejaculatory duct has a diverticulum.

From the foregoing it is evident that specimens of *Mesostoma ehrenbergi* identical with European descriptions are widely spread in the United States. Curiously enough, the material from the Genesee River in northern New York selected by Husted and Ruebush for comparison with European specimens actually appears to differ from the latter in the points mentioned above and therefore could be considered a subspecies but in no case is the name *wardii* applicable. The original description of *Mesostoma wardii* (Woodworth, 1896) is so poor as to be utterly unrecognizable and was later repudiated as a distinct species by the author himself (Woodworth, 1897).

The literature does not contain a good figure of the penis of *Mesostoma ehrenbergi*. Luther's (1904) excellent figures give a series of sections of the penis but not of the organ as a whole. Because of the marked curvature of the penis one is unlikely ever to obtain a median sagittal section, and this no doubt explains the omission of a figure by preceding authors. Although I also failed to obtain an exact median section, I have been able to work out the form of the penis by a study of several series of sections and present figure 17. Typically in *Mesostoma* seminal and prostatic parts are enclosed in the penis bulb, but *ehrenbergi* is peculiar in the separation of those two parts. Here the penis bulb is purely seminal. It is an oval structure entered at its proximal end by the sperm ducts, swollen into vesicles packed with sperm. The wall of the penis bulb is thinner and less muscular than usual in the genus but apparently of firmer consistency. The usual muscle layers are not much in evidence. At its distal end the penis bulb narrows and curves to enter the prostatic vesicle which lies parallel to the bulb. The ejaculatory duct lies against the convexity of the curve, but assumes a central position in the prostatic vesicle. A bunch of prostatic glands enters the proximal end of the prostatic vesicle on the convex side of the curve. The interior of the prostatic vesicle is subdivided into radiating chambers of secretion. Near the distal end of the prostatic vesicle, the ejaculatory duct presents a diverticulum, then enters the rounded, protruding penis papilla, in which it curves to exit on the side away from the penis bulb. Round sections of the penis papilla with its asymmetrical duct are met with in the antrum of all series of sections (fig. 16).

After studying the penis of *M. ehrenbergi,* I suddenly realized that it closely resembles that of *M. macropenis,* which I described from Douglas Lake, Michigan, some years ago (Hyman, 1939a). In fact it now appears that *macropenis* can be at best only a subspecies of *ehrenbergi.* Reëxamination of the scanty available material of *M. macropenis* reveals that the testes are more lobulated than in the original figure, but the yolk glands are so poorly indicated in the material that no conclusion can be drawn about them. Probably what were considered yolk glands in the original description are in fact embryos. *Mesostoma macropenis* seems to be a dwarf variant of *M. ehrenbergi.* Despite the small size of all the available specimens, sexual maturity must be assumed, as the seminal vesicle is filled with sperm and the seminal receptable contains sperm, an indication that copulation had occurred. None of the specimens (three whole mounts, one set of sagittal sections) contain any egg capsules, hence it may be assumed that the specimens were in the stage of producing subitaneous eggs which do not contain much yolk and which are said to be produced before the yolk glands have attained full development.

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